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D. Lapota, D. K. Young, S. A. Bernstein, M. L. Geiger, H. D. Huddell, J. F. Case

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RDT&E Division
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DIEL BIOLUMINESCENCE IN HETEROTROPHIC AND PHOTOSYNTHETIC MARINE DINOFLAGELLATES IN AN ARCTIC FJORD

DAVID LAPOTA*, DAVID K. YOUNG†, STEPHEN A. BERNSTEIN‡, MARK L. GEIGER‖, HOWARD D. HUDDELL‖ AND JAMES F. CASE‖

*Naval Ocean Systems Center, Marine Environment Branch, San Diego, California 92152-5000, USA †Naval Oceanographic & Atmospheric Research Laboratory, Oceanography Division, Stennis Space Center, Mississippi 39529-5004, USA. ‡Marine Sciences Institute, University of California, Santa Barbara, California 93106, USA. ‖Naval Oceanographic Office, Code OWSL, Stennis Space Center, Mississippi 39529-5000, USA

Oceanic and coastal bioluminescence in surface waters, in many instances, is produced by microscopic dinoflagellates. Their light emission is usually observed at a maximum during the night hours and markedly inhibited during the day. This diel periodicity has never been observed *in situ* for identified species and never before in heterotrophic *Protoperidinium* dinoflagellates. Pronounced differences in stimulable bioluminescence measured with bathyphotometers in Vestfjord, Norway in September 1990 correlated with simultaneous ship-board laboratory experiments. Cells of both the photosynthetic *Ceratium fusus* and heterotrophic *Protoperidinium curtipes* showed a pronounced inhibition of bioluminescence during the day and maximum bioluminescence at night.

INTRODUCTION

Oceanic bioluminescence in the surface waters of the world's oceans is produced by numerous microscopic photosynthetic and heterotrophic dinoflagellates (Kelly & Katona, 1966; Kelly, 1968; Tett, 1971; Tett & Kelly, 1973; Kelly & Tett, 1978; Filimonov & Sadovskaya, 1986; Lapota *et al.*, 1988). Their light emission is at a maximum during scotophase (night hours) with minimal light emission expressed during photophase (day hours). This light-controlled diel periodicity in bioluminescence has been observed repeatedly in the field for mixed populations of dinoflagellates (Backus *et al.*, 1961, 1965; Clarke & Kelly, 1965; Kelly & Katona, 1966; Kelly, 1968; Yentsch & Laird, 1968; Lapota *et al.*, 1988) and in laboratory measurements of cultured photosynthetic dinoflagellates (Haxo & Sweeney, 1955; Sweeney & Hastings, 1957; Hastings & Sweeney, 1958; Bigelow *et al.*, 1969; Sweeney, 1979) but never *in situ* for identified populations, and never before in heterotrophic *Protoperidinium* dinoflagellates. Pronounced differences in stimulable bioluminescence, most recently measured with two bathyphotometers at the surface and at depth between midday and midnight in Vestfjord, Norway, correlated with simultaneous ship-board laboratory experiments. Both the photosynthetic cells of *Ceratium fusus* (Ehrenberg) Dujardin and the heterotrophic dinoflagellate *Protoperidinium curtipes* Jorgensen showed a pronounced inhibition of bioluminescence during photophase and maximum bioluminescence during scotophase.

Measurements completed earlier during the Northern Lights expedition revealed that the dominant light producing plankton were *G. tusus* and *P. cuttipes*. These observations permitted us to hypothesize that the field effects we measured may be attributed to the diel rhythms of bioluminescence expressed in these species. To verify these observations we tested dinoflagellate cells of both species for their diel changes in bioluminescent response in the ship's laboratory particularly when marked increases in bioluminescence were measured *in situ*. In the field this was marked by the onset of sunset or sunrise. A newly developed bathyphotometer, High Intake Defined Excitation (HIDEX), able to measure the vertical distribution of bioluminescence from the surface to a depth of 100 m, was deployed prior to sunset (approximately 1830 local time) to measure changes in bioluminescence during increased darkness. The object of these activities was to measure the change in light output in both dinoflagellate species from sunset into the dark hours, and to verify these laboratory measurements with concurrent field bathyphotometric measurements.

MATERIALS AND METHODS

Bathyphotometer and ship-board measurements

Bathyphotometer casts of the vertical distribution of bioluminescence were made in Vestfjord, Norway at 68°15'N 15°49'E. A night profile cast was conducted at 2314 13 September 1990 and a day profile was conducted at 1400 the following day. Bathyphotometer casts conducted near midnight at this station and at other stations within Vestfjord showed that maximum bioluminescence increased no more than 20% following the rapid increase in bioluminescence following dusk. The descent of the bathyphotometer from the surface to a depth of 92 m at night and 100 m during the day was 7 min (2·3-2·4 m resolution). Bioluminescence was measured by pulling sea-water past an RCA 8575 photomultiplier tube (PMT) operating in the photon count mode. PMT pulses were integrated every 10 s during the descent and ascent with a real-time output displayed on a computer as average counts s^{-1}, later converted to photons s^{-1} ml^{-1} of sea-water. Sea-water temperature was also measured with a Sea Bird temperature probe (Model SBE-3) while chlorophyll fluorescence was measured *in situ* with a Sea Tech fluorometer. This version of the bathyphotometer has been described (Lapota *et al.*, 1989). The bathyphotometer was calibrated with the luminous bacteria *Vibrio harveyi* and solutions of the bacterium at several known source strengths were measured in the sample chamber of a Quantalum detector (Matheson *et al.*, 1984). Multiple profiles to measure stimulated bioluminescence during the dusk hours on 25 September were made using the HIDEX bathyphotometer developed at the University of California, Santa Barbara. The high flow characteristics (20 l of sea-water s^{-1}) and large light-integrating chamber of the system make it possible to do high speed profiles with significant reproducibility (Case *et al.*, 1990).

Two ship-board photometer systems also measured stimulated bioluminescence within a darkened flow through chamber. The intake pipe within the sea chest, located in the engine room of the ship, was positioned through the ship's hull at a 3 m depth

During the night and midday casts sea-water temperature was mixed to a depth of 40 m. A strong thermocline was measured at this depth, the temperature decreasing from 13 C at 40 m to 6 C at 90 m (Figure 2A). Chlorophyll fluorescence displayed a similar trend in the mixed layer and peak chlorophyll concentrations were similar for both day and night (0.6-0.7 µg l⁻¹ chl); however, the midday peak was measured at a depth of 25 m while the night measurements displayed two layers at 20 m and 35 m (Figure 2B).

During the dusk time-series conducted with HIDEX on 25 September, maximum bioluminescence was always measured at a depth of 32 m from the start (1830) to the end (2120) of these measurements (Figure 3). Bioluminescence increased six-fold during the seven profiles conducted in less than 3 h. Maximum stimulable bioluminescence increased to 3×10^8 photons s^{-1} ml^{-1} sea-water during the course of the early evening.

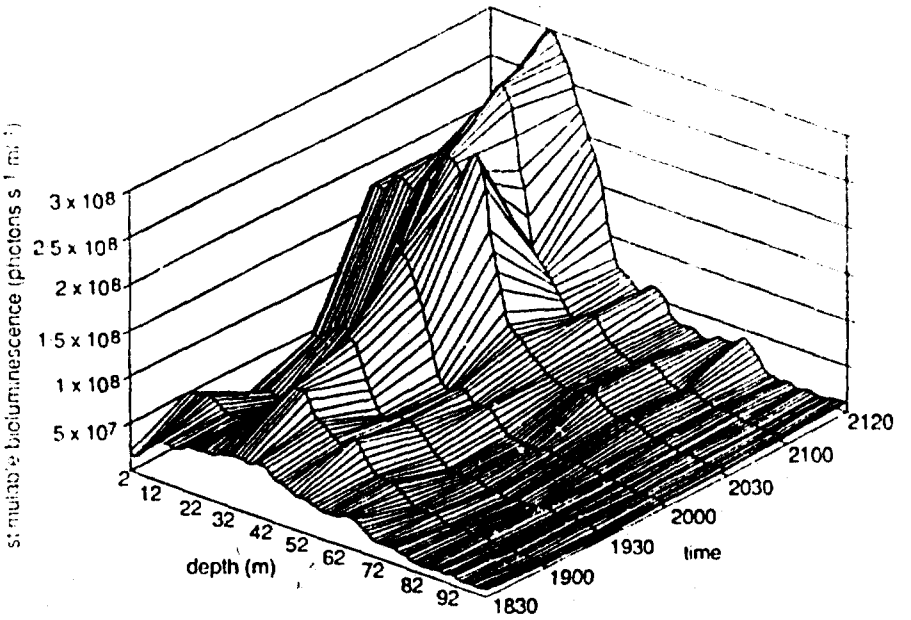

Figure 3. Multiple profiles of measured bioluminescence using the UCSB HIDEX bathyphotometer at Station 6 in Vestfjord, Norway. Seven profiles were conducted in less than 3 h during this dusk time series. Maximum bioluminescence was always measured at a depth of 32 m in this series.

Plankton analysis and light budgets

Maximum numbers of dinoflagellates (1759 cells l^{-1}) at midday (Figure 4A) were observed at a depth of 10 m below the sea surface while maximum numbers of dinoflagellates at night (1842 cells l^{-1}) were collected at a depth of 25 m at night (Figure 4B). Bioluminescent dinoflagellates followed similar trends; however, their numbers represented only 6 and 9% of all dinoflagellates for the midday and night casts respectively. Dinoflagellates decreased markedly below the thermocline. There were 16 and 25 times fewer dinoflagellates at 50 m than at 40 m for both the midday and night casts, respectively.

The depth distribution of the luminescent *Ceratium* and *Protoperidinium* dinoflagellates differed with respect to midday and night casts. Maximum numbers of *C. fusus* (92

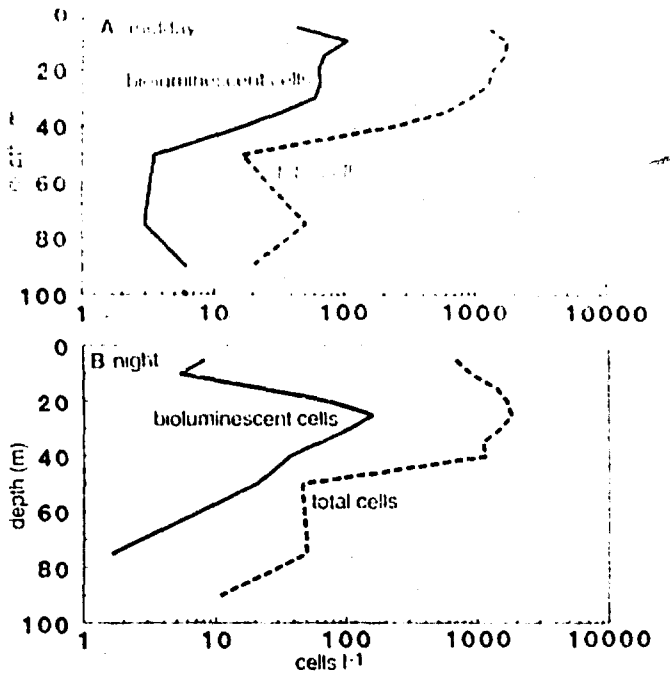

Figure 4. Total dinoflagellates and bioluminescent dinoflagellates collected at (A) midday and (B) night at Station 6, 13 September 1990. The maximum number of cells for both components was 20 m shallower at midday than at night.

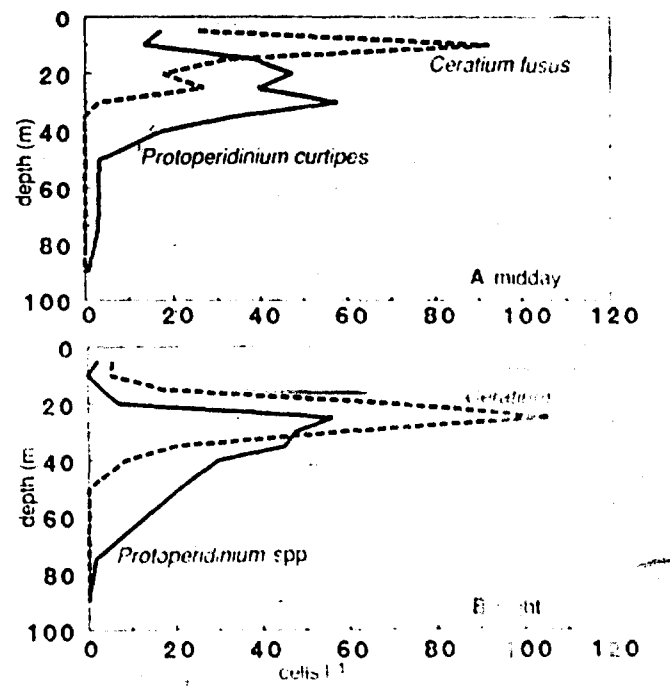

Figure 5. The vertical distribution of the bioluminescent dinoflagellates *Ceratium fusus* and *Protoperidinium* spp. during (A) the midday cast and (B) the night cast. Maximum numbers of *Protoperidinium* dinoflagellates remained unchanged at 30 m, for either midday or night.

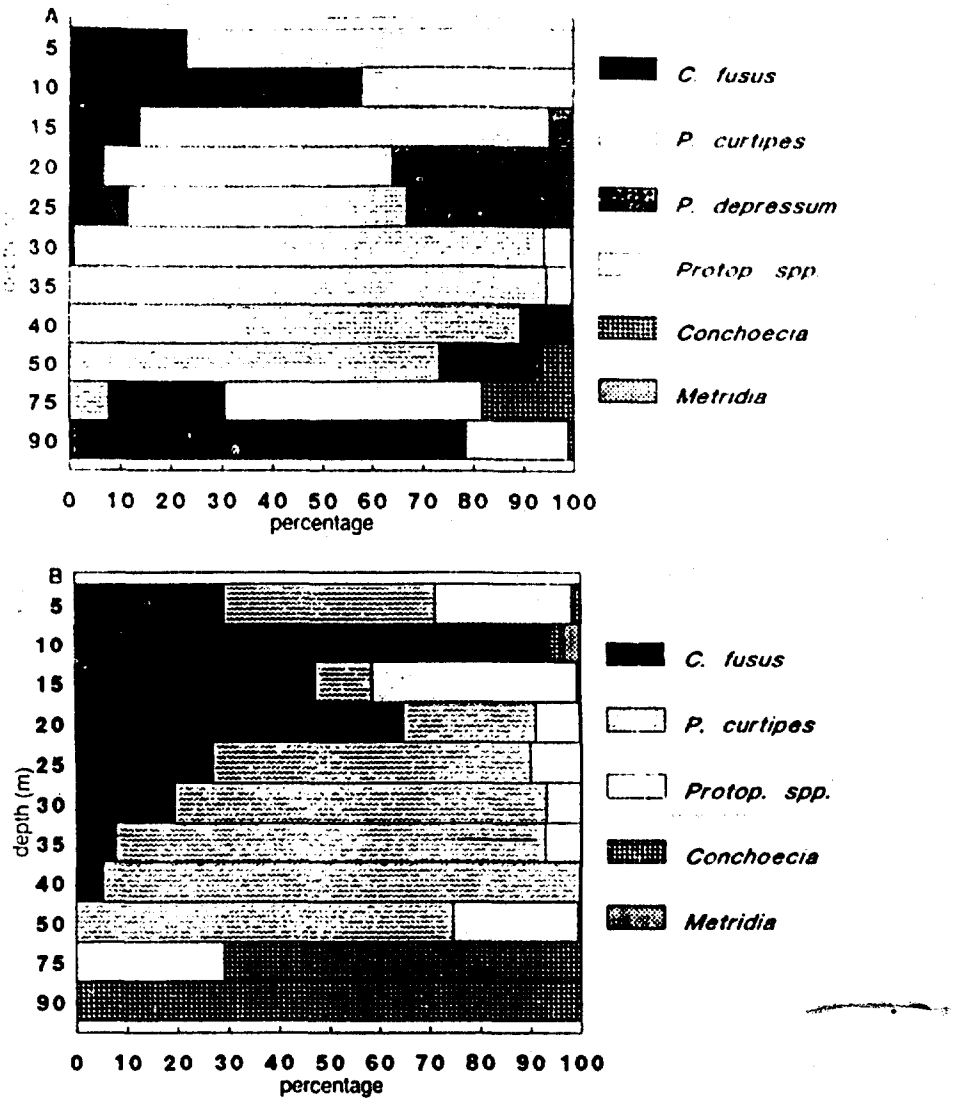

Figure 6. Calculated bioluminescent light budgets for (A) the midday cast and (B) the night cast. The common feature between the two budgets is the dominant contribution by *Ceratium fusus* at the shallow depths replaced by *Protoperidinium curtipes* with increasing depth. Both *Conchoecia* and *Metridia* increased their impact on the light budget at night.

cells l^{-1}) were collected at a depth of 10 m for the midday cast (Figure 5A) while maximum numbers of these cells were collected at a depth of 25 m (106 cells l^{-1}) for the night cast (Figure 5B). *Protoperidinium* spp. dinoflagellate cells remained fairly constant in abundance between casts (56-58 cells l^{-1}) at a depth of 30 m (Figure 5). Light budgets were constructed for profiles from the pumped samples for both the midday and night casts, and bioluminescent crustaceans were collected in the vertical net tows and their contribution to the light budget calculated (Figure 6). Both *Metridia longa* and *M. lucens* copepods and the ostracod *Conchoecia elegans* were the dominant light-producing

zooplankton. Furcilia of *Meganyctiphanes* were intermittently present in low numbers. Both light budgets were dominated by *C. fusus* and *Protoperidinium* dinoflagellates within the upper 50 m. *Conchoecia* and *Metridia* dominated the light budgets at 75 and 90 m below the sea surface.

Laboratory measurements

Ceratium fusus exhibited minimum and maximum mean light output values of 2×10^{7} (1200) and 1×10^{9} (0200) photons cell^{-1}, respectively (stimulable light per 40 s). *Protoperidinium curtipes* exhibited minimum and maximum mean light output values of 2×10^{6} (1200) and 5×10^{9} (0200) photons cell^{-1}, respectively (stimulable light per 40 s). The largest rates of change in bioluminescence intensity for *C. fusus*, in the laboratory, occurred between 1700 and 1800, while that of *P. curtipes* occurred later, between 1800 and 2000. Over these time intervals *Ceratium* increased its mean light output 29-fold while *Protoperidinium* increased its mean light output 137-fold. *Protoperidinium curtipes* emitted about five times more light than *C. fusus* at 0200. In contrast, laboratory cells of *P. curtipes* decreased their light output 47-fold between 0400 and 0600, while light output in *C. fusus* diminished 1760-fold following sunrise at approximately 0600 (Figure 7). *Ceratium fusus* emitted 53 times more light at 0200 than 1200, while *P. curtipes* produced 2700 times more light at 0200. Night light-output values for both *C. fusus* and *P. curtipes* in this study fall within the same range of intensity for other coastal dinoflagellate species observed in previous studies (Table 1).

Ship-board measurements

Field measurements of surface bioluminescence were recorded for more than 30 h with ship-board photometers. The diel periodicity from one day to the next is apparent in Figure 8, as minimal intensity was measured from 1200 to 1300, while maximum intensity occurred from 2000 to 0400. Maximum bioluminescence levels ranged from 1-3×10^{8} photons s^{-1} ml^{-1} of sea-water while minimum bioluminescence was 2-3×10^{5} photons s^{-1} ml^{-1} sea-water. The three orders-of-magnitude change near the surface in the field is consistent with cells tested in the laboratory. Bioluminescence at the surface increased

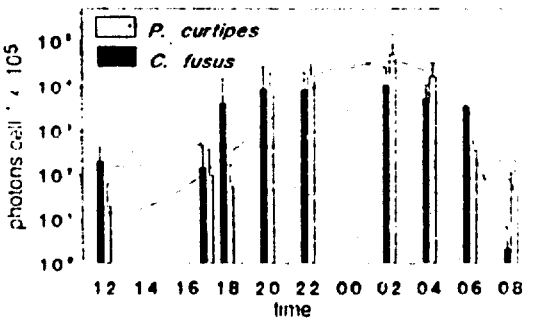

Figure 7. The diel variation of bioluminescence in isolated dinoflagellate cells measured in the ship's laboratory. A third-order polynomial curve was fitted through the mean values to exhibit the diel character of bioluminescence in both *Ceratium fusus* and *Protoperidinium curtipes*. The error bars represent two standard deviations from the mean value.

Table 1. *Range of dinoflagellate light output values per cell for some commonly found coastal dinoflagellates. Most values represent total light from a single cell or mean light output derived from groups of cells by mechanical stimulation.*

Species	Light output (photons)	Reference
[illegible]	2x10	Lapota [illegible]
	9x10	Esaias [illegible]
Gonyaulax polyedra	1x10	Biggley *et al.* (1969)
	1x10 - 2x10	Krasnow *et al.* (1981)
	6x10 - 1x10	Sweeney (1981)
Protoperidinium depressum	2x10	Lapota *et al.* (1989)
P. pentagonum	4x10	Esaias *et al.* (1973)
P. curtipes	3x10	Lapota *et al.* (1989)

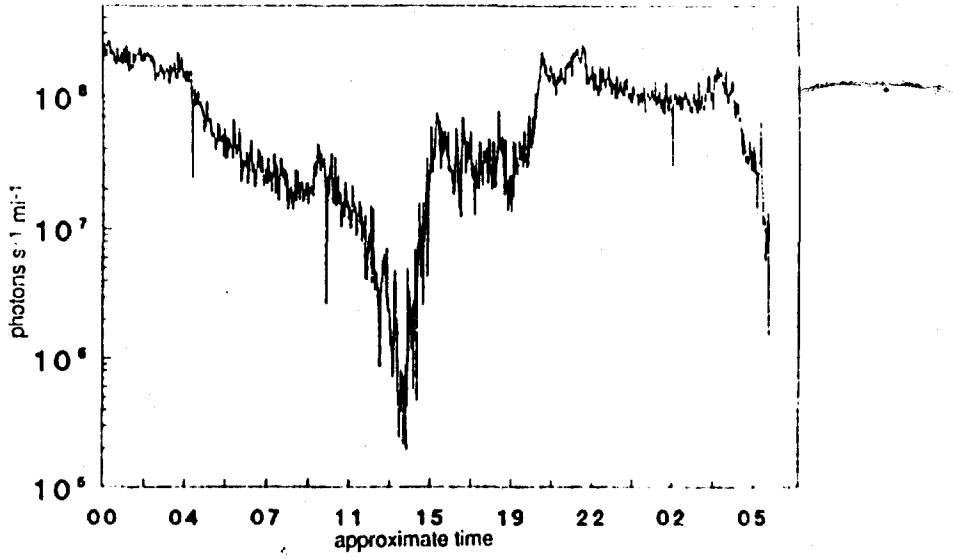

Figure 8. The diel periodicity of bioluminescence within Vestfjord, Norway at a 3-m depth at Station 6 for 30 h (1158 on 24 September to 0615 on 26 September 1990). Maximum bioluminescence was maintained throughout the night following minimum levels of bioluminescence, and ranged from 1x10⁶ to 3x10⁸ photons s⁻¹ ml⁻¹ sea-water.

from 1300 to approximately 5x10⁷ photons s⁻¹ ml⁻¹ sea-water at 1800. Bioluminescence at sunset increased by a factor of four at a depth of 32 m (Figure 3). This same trend was also measured at the sea surface and bioluminescence increased two-fold in intensity from 2030-2120 at depth and remained at 3x10⁸ photons s⁻¹ ml⁻¹ sea-water throughout the night hours.

DISCUSSION

The greatest rates of change in light output for the laboratory cells coincide with depth and surface field measurements. The lack of increased bioluminescence below 50 m during this period would support the hypothesis that the measured diel luminescence

is dinoflagellate in origin and preclude the hypothesis that bioluminescent zooplankton migrating to shallower depths at night contribute significant levels of light (Figure 3). The luminescent copepods *Metridia longa* (Lubbock) and *M. lucens* Boeck were collected in our pumped samples and net tows. However, there is no evidence that these and similar bioluminescent copepods exhibit any diel rhythm in light output (Evstigneev & Bityukov, 1986; Herring, 1988). Avoidance of the detector by these copepods is unlikely because of the large volumes of water which the HIDEX bathyphotometer pulls into its sampling chamber (20 l sea-water s^{-1}). These copepods discharge 2–3 orders of magnitude more light than do dinoflagellates (Lapota *et al.*, 1989). If sufficient numbers of these copepods were present throughout the water column, then the diel periodicity we measured should have been greatly dampened or eliminated entirely. Additionally, analysis of the net tows at these depths indicates that the low numbers of *Metridia* collected (<1 m^{-3}) made minimal contributions to the light budget calculated for dinoflagellates and zooplankton. There are similar trends for both calculated light budgets as expected, based on the similarity of bioluminescent dinoflagellates, copepods, and ostracods. Both budgets were constructed for the night phase; however, the midday light budget would actually look quite different because photoinhibition would reduce the light output of both species of dinoflagellates at the ocean surface to levels comparable to laboratory measurements (Figure 7). These inhibition factors may be less for cells found at greater depths because of decreased ambient light levels. The midday bioluminescence cast should certainly reflect these photoinhibition processes, coupled with the extremely low numbers of luminescent ostracods and copepods collected in our nets.

Differences in the vertical distribution of the luminescent *Ceratium fusus* and the apparently unchanged peak of bioluminescence measured during either midday or night raises several interesting questions. The first being that at a depth of 30 m, *Protoperidinium curtipes* is the major light-emitter, either at midday (although at a much reduced intensity) or during the night, if one examines the cell distributions (Figure 5) or the light budget (Figure 6). The other aspect, which may not be reflected in the midday bioluminescence profile (Figure 1), is the shallower distribution of *C. fusus* at midday than at night, which might imply a vertical migration by these cells up to a depth of 10 m below the sea surface as opposed to their 25-m peak layer night distribution. There is substantial evidence for circadian rhythms in the vertical migrations of dinoflagellates (Levandowsky & Kaneta, 1987). Cells of *Ceratium furca* were observed to migrate rhythmically up and down in a laboratory culture in complete darkness for six days (Weiler & Karl, 1979) and *C. fusus* has been observed to swim at speeds from 0·23 to 1 m h^{-1} (Peters, 1929; Hasle, 1964). It is possible that our sampling has detected the diurnal migration of *C. fusus* and other *Ceratium* dinoflagellates (Figure 4).

The diurnal variation of bioluminescence has not been demonstrated in isolated cells of either *C. fusus* or *P. curtipes* with concurrent field measurements. While photoinhibition of bioluminescence in several species of *Protoperidinium* was demonstrated in the laboratory using lamps of varying spectra and intensity, a diel variation of bioluminescence has never before been demonstrated in recently isolated field populations of *P. curtipes* (Filimonov & Sadovskaya, 1986; Tyul'kova & Filimonov, 1981). It appears that *P. curtipes* may be more photoinhibited by ambient light conditions at midday than the

photosynthetic cells *C. tasus*. However, *P. curtipes* emitted five times more light per cell at night (Figure 7). Surface bioluminescence (Figure 8) and laboratory measurements (Figure 7) might also reflect a circadian rhythm of bioluminescence independent of external light levels. Bioluminescence decreased while still dark before sunrise at 0600 (Figure 8).

The laboratory measurements confirm the temporal field measurements of minimum and maximum intensity, the periods of increasing and decreasing bioluminescence, and the diel change in bioluminescence. Both laboratory and *in situ* measurements, while quite different in execution, have identified similar trends within the data sets. Individual variations in the range of intensities (from midday to midnight) from location to location is certainly a reflection of the diel bioluminescence change inherent in each species, and to the composition of the species present spatially and temporally. Both methods (field and laboratory) produce a consistent picture of the nature of diel periodicity of bioluminescence in these species.

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